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AND ITS APPLICATION ON HAWAIIAN BOTTOMFISHES

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ABSTRACT

To help prevent recruitment overfishing of the Hawaiian bottomfish stocks, the Bottomfish and Seamount Groundfish Management Plan Monitoring Team of the Western Pacific Fishery Management Council proposed a definition of overfishing that is intended to be an amendment to the Bottomfish Fishery Management Plan. The definition states that overfishing occurs when a measure of the spawning stock biomass, expressed as a proportion of the virgin biomass, is less than 0.20. This measure, which is known as the spawning potential ratio (SPR), was calculated for five bottomfishes from the main Hawaiian Islands: opakapaka, *Pristipomoides filamentosus*; onaga, *Etelis coruscans*; ehu, *Etelis carbunculus*; uku, *Aprion virescens*; and ulua, *Caranx ignobilis*. Two different estimators of SPR were considered, the equilibrium and dynamic estimators. The equilibrium estimator requires estimates of growth and mortality and predicts a value of SPR that would occur if the population were at equilibrium. The dynamic estimator requires a time series of catch, effort, and size data extending back to the initiation of the fishery and measures the existing value of SPR. Values of equilibrium SPR could be calculated for only opakapaka and ehu, whereas values of dynamic SPR could be calculated for all five species. Most values of the equilibrium and dynamic SPRs were between 0.21 and 0.31, indicating that the spawning biomasses are generally low but not below the critical value defining overfishing.

INTRODUCTION

A recent revision to the "Guidelines for Fishery Management Plans (50 CFR Part 602)" included a new provision that each fishery management plan (FMP) must contain "an objective and measurable definition of overfishing," where overfishing in this context was intended to mean recruitment overfishing or the failure to maintain sufficient brood stock to provide continued replenishment of young fish. In response to this revision in the guidelines, the Bottomfish and Seamount Groundfish Management Plan Monitoring Team (PMT) of the Western Pacific Fishery Management Council proposed the following definition of overfishing: A bottomfish species is overfished when the spawning potential ratio (SPR; Goodyear 1989), or the ratio of the spawning stock biomass per recruit at the current level of fishing ($SSBR_f$) to the spawning stock biomass per recruit that would occur in the absence of fishing ($SSBR_u$), is ≤ 0.20. This definition is consistent with the objectives of the revised guidelines and is nearly identical to the overfishing definitions that have been independently developed and proposed for other FMPs (e.g., Amendment No. 1, Reef Fish FMP, Gulf of Mexico Fishery Management Council).

Besides defining overfishing in terms of SPR, the PMT also specified how SPR was to be calculated. To allow for differing availability of data among the various species and areas, two estimators of SPR were proposed, the equilibrium and dynamic estimators. The equilibrium estimator of SPR is based on yield-per-recruit theory (Beverton and Holt 1957) and assumes that the rate of fishing and the size range of fish harvested have remained or will remain constant long enough for the population to be considered in equilibrium. Although this estimator is widely used (Beddington and Cooke 1983; Polovina 1987; Goodyear 1989), it requires estimates of growth and mortality rates and thus may be difficult to calculate in tropical areas where the ageing of fishes is often problematical. If these vital rates can be estimated, however, the equilibrium estimate of SPR has an advantage of being calculable from current data alone and therefore applicable to situations where a time series of data is lacking. By comparison, the dynamic estimator of SPR is based on the change in the catch per unit effort (CPUE) of mature fish relative to that at the initiation of the fishery and is a direct estimate of the relative spawning biomass rather than a theoretical approximation to its value at population equilibrium. On the other hand, a dynamic estimate of SPR requires a historical record of both CPUE and size distribution extending back to the initiation of the fishery, and such historical data are often unavailable. Thus, the relative utility of the two estimators will vary depending upon the type and amount of available data.

In this paper, we calculate, when possible, both estimators of SPR for the five principal bottomfish species from the main Hawaiian Islands (MHI): opakapaka, *Pristipomoides filamentosus*; onaga, *Etelis coruscans*; ehu, *Etelis carbunculus*; uku, *Aprion virescens*; and ulua, *Caranx ignobilis*, to determine which estimator is better for MHI bottomfishes and whether any of the species should be considered overfished under the new definition.

MATERIALS AND METHODS

Data Sources and Preliminary Analysis

Estimates of SPR were calculated from two primary types of data: sales data obtained by National Marine Fisheries Service personnel at the Honolulu fish auction during 1986-88 and catch reports submitted by bottomfish fishers to the Hawaii Department of Land and Natural Resources (DLNR) during 1947-87. Sales data consist of the total weight and number of fish within auction lots, where a lot is composed of one or more individuals of a single species that have been sorted to uniform size (Ralston et al. 1986). Because of this sorting, sales data can be used to construct nearly unbiased size-frequency distributions of each species (Ralston et al. 1986). Such size-frequency distributions were computed as follows. Sales data were first separated by area (i.e., MHI and Northwestern Hawaiian Islands (NWHI)). A weight-frequency distribution for each species, area, and year was then constructed by summing the mean weight of individual lots, weighted by the number of fish in the lot. A length-frequency distribution was constructed from each weight-frequency distribution by using the length-weight equations provided in Uchiyama et al. (1984). Weight-frequency and length-frequency distributions for each species and area were then averaged over the 3 years (1986-88) to reduce the effects of sampling error and recruitment fluctuations.

The DLNR catch reports consist of the daily total weight and number of each species caught by each vessel. Since both large and small individuals of the same species are included in the daily estimate of total weight, the catch reports cannot be used to obtain an accurate representation of size distribution, but they can be used to estimate catch per day (CPUE). One complication to obtaining such estimates, however, is that some fishers apparently report catch on a per-trip rather than a per-day basis. This complication can be eliminated by considering only CPUE data from the MHI, where trip lengths are almost always only 1 day. Annual mean CPUE was computed, either considering all bottomfish species combined or each of the five major species separately, after eliminating the following categories of data. First, all catches obtained in the NWHI were eliminated because trips lengths were greater than 1 day. Second, all catches of kahala, *Seriola dumerili*, were eliminated to remove the effect of a sharp drop in market demand that occurred in the 1970s after this species was implicated as an occasional carrier of ciguatoxin. Third, catches from trips not devoted exclusively to bottomfishing (i.e., trips with a total catch <90% by weight of bottomfish species) were eliminated to remove the ambiguity in the allocation of effort expended in a single trip between pelagic, reef, and bottomfish species. Fourth, all catches from vessels whose greatest catch within a single year was <30% of the highline catch were excluded to eliminate small, presumably part-time vessels. The annual highline catch was calculated by ranking all vessels according to their highest catch of the year, then computing the average of the 10 highest of these catches.

Calculating Equilibrium SPR

Equilibrium SPR is usually calculated as the ratio of $SSBR_f$ and $SSBR_u$ estimates (Beddington and Cooke 1983; Polovina 1987). This approach, however, requires values for a variety of population parameters: fishing mortality (F), natural mortality (M), the rate constant (K) and asymptote (L_∞) of the von Bertalanffy growth equation, age at entry into the fishery (t_e), and age at maturity (t_m), all of which are difficult to estimate without adequate age and growth data. Since such data are either lacking or quite meager for all bottomfish species, an alternative approach suggested by Polovina (1987) was used, and the equilibrium estimator of SPR was modified so that 1) SPR was calculated directly rather than as a ratio of SSBR estimates; 2) F, M, and K were expressed as composite parameters (i.e., F/K, M/K); and 3) t_e and t_m were expressed as their equivalent lengths l_e and l_m. When this was done, the resulting estimator is (see Appendix A for a complete derivation)

$$SPR = \left(\frac{L_\infty - l_e}{L_\infty - l_m} \right)^{-F/K} \frac{\sum_{n=0}^{3} \frac{\Omega_n \, (1 - l_m/L_\infty)^n}{F/K + M/K + n}}{\sum_{n=0}^{3} \frac{\Omega_n \, (1 - l_m/L_\infty)^n}{M/K + n}} ; \qquad (1)$$

where $\Omega_n = 1, -3, 3, -1$ for $n = 0, 1, 2, 3$.

Values of F/K, M/K, and L_∞ needed to evaluate this equation were estimated for each species from averaged length-frequency data. This was done by using a procedure developed by Wetherall et al. (1987) that estimates Z/K (i.e., $F/K + M/K$) and L_∞ from the regression of the mean length of all fish $\geq l_{ci}$ on l_{ci}, a cutoff length ranging from the first length category that is fully selected by the fishery (L_c) to the largest length category. L_c was chosen in a manner similar to that of Polovina (1987, 1989) and Ralston and Kawamoto (1988) and set at 1 cm larger than the modal length. Values of Z/K and L_∞ were first estimated by applying the regression method to MHI data, then assuming that the relatively new fishery in the NWHI has not yet substantially influenced the size distribution of fishes, values of M/K and L_∞ were estimated by applying the method to data from the NWHI. A value of F/K was estimated as the difference of Z/K and M/K, and a value of L_∞ was estimated as the average of the MHI and NWHI estimates.

Values of the size at entry to the fishery, l_e, were estimated by assuming that size selection increases linearly with length from 0.00 at 1 cm less than the length interval containing the smallest individual to 1.00 at 1 cm greater than the modal length. The value of l_e was then estimated, by interpolation, as the size at which selection equals 0.50.

For opakapaka alone, additional estimates of L_c and l_e were computed from the ratio of the number of fish in each length interval caught by the commercial fishery to the number caught by random sampling on 17 cruises of

the NOAA ship *Townsend Cromwell* to the NWHI in 1978-81. Since the fishing gear used for scientific sampling was nearly identical to that used by commercial vessels, differences in length distribution were assumed to be the result of targeting by fishers. Size selection was described by using a three-parameter logistic curve. The parameters of the logistic curve were estimated by using nonlinear regression to fit the following model:

$$N_{ci} = \frac{C}{1 + Ae^{-Bi}} N_{si} \; ; \qquad (2)$$

where N_{ci} and N_{si} is the number of i cm fish in the commercial and scientific data and A, B, and C are undetermined regression coefficients. After the coefficients were estimated, C was set to 1.0, and the resulting selection equation was then evaluated at 0.95 to estimate L_c and, assuming the "knife-edge selection" approximation (Beverton and Holt 1957), evaluated at 0.50 to estimate l_e.

Values of l_m were obtained for ehu (Everson 1984), opakapaka (Kikkawa 1984), ulua (Sudekum 1984), uku, and onaga (Everson et al. in press). The values of l_m chosen for use in this study were for females and were specified as the size at 50% maturity.

Estimates of Z/K and L_∞ obtained using the Wetherall procedure (Wetherall et al. 1987) can be highly biased if the population from which the length-frequency samples were drawn is not in equilibrium (Somerton and Koybashi in prep.). To determine whether the MHI and NWHI populations of bottomfishes departed sufficiently from equilibrium to have a substantial effect on the estimates of Z/K and L_∞, we used the chi-square test proposed by Somerton and Koybashi (in prep.). This test, which measures the differences among three successive years of length-frequency data, was conducted for each species in each area as follows: (1) The annual length-frequency distribution for each of 3 years (1986-88) was multiplied by a correction factor consisting of the total number of lots in the sample divided by the total number of fish, so that the sum of the frequencies would be equivalent to the degrees of freedom (i.e. number of lots). (2) L_c was determined for each year, then the length-frequency distributions from all 3 years were left truncated at the largest of the L_c values. (3) l_{max}, or the largest length interval with at least five observations, was determined for each year, then all length intervals larger than the smallest of the l_{max} values were pooled into the smallest l_{max}. (4) An l_{max}-L_c by three-contingency table was constructed, and a typical chi-square test of homogeneity was then conducted. Significance of the test indicates the parameter estimates are likely influenced by disequilibrium bias.

Calculating Dynamic SPR

The dynamic estimator of SPR is a ratio of two estimates of relative spawning stock biomass, each of which is measured by the product of CPUE

and the proportion of the catch, corrected for size selection, that is mature. This is expressed as

$$SPR = \frac{U_f \, P_f}{U_u \, P_u} , \qquad (3)$$

where U_f and U_u are the current (fished) and initial (unfished) CPUE and P_f and P_u are the current and initial population correction coefficients. P is calculated as $P = P_m/P_s$, where P_m is the proportion, by weight, of the catch composed of mature fish and P_s is the proportion of mature fish selected by the fishery. P_m is calculated as

$$P_m = \frac{\sum_{i=l_m}^{\infty} w_i}{\sum_{i=l_{min}}^{\infty} w_i} , \qquad (4)$$

where w_i is the total weight of the catch in length interval i and l_{min} is the length of the smallest fish in the catch. P_s is calculated as

$$P_s = \frac{\sum_{i=l_m}^{\infty} w_i}{\sum_{i=l_m}^{\infty} w_i/s_i} , \qquad (5)$$

where s_i is the proportion of length interval i selected by the fishery. Values of s_i were determined for every species with the linear selection model described above and additionally for NWHI opakapaka with the logistic selection model. To reduce sampling variability, U_f was computed as the average CPUE over the 3-year interval 1986-88, and U_u was computed as the average CPUE over the 3-year interval 1947-49. In both cases, U was computed in terms of the aggregate catch rather than the catch of individual species, because of the likelihood of changes in species targeting over time.

RESULTS AND DISCUSSION

Equilibrium SPR

Equilibrium SPR could not be calculated for two species and is likely biased for at least two others (Table 1). For uku, which is primarily restricted to the MHI, length-frequency samples from the NWHI were too few to obtain Wetherall estimates of M/K (Fig. 1). For ulua, which has little market value when it is large, selectivity by the fishery for small

sizes in the MHI (Fig. 1) resulted in a poor fit of the regression line to the size-frequency data. For onaga and initially for opakapaka, estimates of Z/K seemed too small or estimates of M/K and L_∞ seemed too large to be unbiased. Such biases could be due to violations of either of two important assumptions of the Wetherall procedure.

First, the Wetherall procedure assumes that length-frequency samples were drawn from a population in equilibrium; that is, a population that has not experienced recent changes in either recruitment or fishing effort. Somerton and Kobayashi (in prep.) examined some consequences of violations of this assumption and found that estimates of Z/K and L_∞ could be highly biased, depending upon the characteristics of the equilibrium perturbation. To determine whether our estimates could be influenced by such disequilibrium bias, we used the chi-square test described in Somerton and Kobayashi (in prep.). For the three species that were not initially excluded from analysis, the results of the test were as follows:

	MHI results		NWHI results	
Species	P	d.f.	P	d.f.
Opakapaka	0.041	64	0.005	16
Onaga	<0.001	86	0.379	20
Ehu	0.120	60	0.532	30

Since significance (i.e., $P < 0.05$) indicates a high likelihood of bias in the estimates of Z/K and L_∞, the estimates of SPR, which are derived from the estimates of Z/K and L_∞, are likely to be biased for both opakapaka and onaga but not for ehu.

Second, the Wetherall procedure assumes that the value of L_c used in the regression is indeed the size of complete selection by the fishery. Somerton and Kobayashi (in prep.) also examined some consequences of violations of this assumption and again found that Z/K and L_∞ could be highly biased, depending on the true values of Z/K and L_∞ and the direction and magnitude of the departure between the true and assumed value of L_c. Since it is rarely possible to estimate the functional relationship describing the size selection of fishing hooks (Ralston 1990), we initially chose instead the same approach as Polovina (1987, 1989) and Ralston and Kawamoto (1988) and set L_c as 1 cm greater than the modal length. Based on experiments with a length-based simulation model for opakapaka, however, we have found that L_c values chosen in this manner can be quite deviant from the true L_c. To avoid introducing bias due to an improper choice of L_c, it is therefore important to objectively determine L_c, and the best way of doing this is to estimate the size selection function of the fishing gear by comparing the size distribution of fish caught by the commercial fishery to the size distribution of fish caught by a gear with a smaller size of selection.

We were able to obtain such an estimate of the size selection function, at least for one species, using length-frequency data with a small size of selection collected on research cruises of the *Townsend Cromwell* in the NWHI. Of the five species, only two, opakapaka and ehu, had sample sizes sufficiently large to construct reliable scientific length-frequency distributions (Fig. 2). For opakapaka, this length distribution includes smaller fish than the commercial length distribution, but for ehu, the scientific and the commercial length distributions are nearly identical (Fig. 2). This between-species difference in the length ranges of scientific and commercial catches probably reflects a between-species difference in the process of size selection. In the scientific catches, the smallest sizes were almost the same for the two species and it is therefore likely that size selection in these samples was determined by some physical aspect of the fishing gear, probably by hook size (Ralston 1982, 1990). In the commercial catches, however, the smallest size of opakapaka is likely determined by fishing strategy rather than hook size because opakapaka are targeted by fishers in the NWHI and fishers actively seek areas having the largest opakapaka available. Since ehu are not targeted, their smallest size should, as in the scientific catches, be determined by hook size. If this interpretation is correct and the size selection by hooks reaches 1.00 at a fairly small size, then the scientific length distribution can be used to determine a size selection function for opakapaka but not for ehu.

We chose a three-parameter logistic function to describe size selection and estimated the parameters of this function as described earlier. L_c was then estimated by evaluating the selection function to determine the length corresponding to a selection of 0.95 (Fig. 2A). This value, 61 cm, was considerably smaller than the L_c of 69 cm determined by the "mode + 1" rule (Fig. 2C). When the Wetherall procedure was applied to the NWHI data for opakapaka, with L_c set at 61 cm, the estimated values of M/K and L_∞ were both considerably less than the previous estimates (Table 1). Although we do not know whether these estimates are free of bias due to an improper choice of L_c, the estimate of M/K is at least less than the estimate of Z/K, and the estimate of L_∞ (75 cm) is more consistent with the size of the largest (83 cm) opakapaka ever captured by scientific sampling in the NWHI (our simulation studies indicate that L_∞ is typically about 95% of the maximum length obtained in samples of reasonable size drawn from a virgin population). Since L_c could not be similarly estimated for ehu and onaga, estimates of Z/K, M/K or L_∞ for these species could contain significant bias.

Dynamic SPR

Values of dynamic SPR could be calculated for all five species of bottomfish (Table 1), but like the equilibrium estimates, the dynamic estimates are probably biased. This bias could have at least four sources. First, the change in CPUE that has occurred over time (Fig. 3) is undoubtedly less than the change in biomass because, over the 40 years of the DLNR time series, vessels have increased their fishing power by using

radar, loran, chromoscopes, and power reels. Such an increase in fishing power would result in an estimate of U_f/U_u that is larger than the ratio of the biomasses, and this, in turn, would result in an overestimate of dynamic SPR.

A second reason why the dynamic SPR estimates are probably biased is that aggregate CPUE may not be a good measure of the relative abundance of individual species. For example, over the 40 years of the time series, aggregate CPUE has declined by about 50%, while ehu CPUE has declined by over 90% and opakapaka CPUE essentially has not declined at all (Fig. 3). Thus, if the CPUE for individual species is used to compute the values of dynamic SPR, then ehu will have a much lower SPR value, and opakapaka a much higher SPR value, than that predicted from the aggregate CPUE. Use of the CPUE of individual species as an index of abundance is always suspect when the fishery catches a mixture of species, because between-species differences in either targetability by fishers or vulnerability to fishing gear result in differences in the proportionality constants equating CPUE to abundance. Since the proportionality constants are canceled in the computation of SPR, however, it is the temporal changes in the proportionality constants that are important. For example, if opakapaka increasingly becomes the main target species of the bottomfish fishery over time, its CPUE will increase, and the CPUE of other species will decrease relative to the values that would have been obtained without targeting. We lack sufficient data to determine whether the observed lack of a decrease in opakapaka CPUE over time is due to such a shift in targeting or due to a higher productivity of opakapaka relative to other species. But it is difficult to believe that opakapaka, which has been the mainstay of the fishery, has escaped significant impact.

A third reason why the dynamic SPR values are probably biased is that the correction of the length-frequency distributions for size selection by the fishery may be inaccurate. We assumed that selectivity increased linearly with length because in nearly all cases we did not have the data to determine the true selectivity function. For opakapaka in the NWHI, however, we did have the appropriate data and therefore were able to examine the adequacy of the linear assumption. Differences in the corrected length distribution resulting from the application of both the linear and the logistic selection models are in Figure 4. Assuming that the logistic model is the more accurate of the two, then using the linear model underestimates s_i at the larger sizes and therefore overestimates spawning biomass. Since this effect is greater in the NWHI, because $l_e > l_m$, the value of SPR will therefore be underestimated (Table 1). For opakapaka, however, the effect of this appears to be small.

A fourth reason why the dynamic SPR values are probably biased is that some MHI fishers apparently select for smaller opakapaka and ulua to satisfy a "pan-fish" market (Fig. 1). Although we are uncertain of its extent, this type of size selection would result in length-frequency distributions that underrepresent large fish, and this, in turn, would result in underestimates of P_m for these species in the MHI.

Equilibrium SPR Versus Dynamic SPR: Which Is Best for MHI Bottomfishes?

Performance of the two estimators should be assessed on the basis of whether they can be calculated with available or easily obtainable data and whether they are unbiased. Based on the first measure, the dynamic estimator is superior because, with available data, it could be calculated for all five species, whereas the equilibrium estimator could be calculated for only two. This is true, however, only because CPUE data are available from an early stage of the MHI bottomfish fishery; such superiority may not exist for areas lacking equivalent data. The second measure cannot be adequately assessed, because we have no independent measure of spawning stock biomass that could be used to judge the probable bias of the two SPR estimates. However, the estimate of equilibrium SPR for opakapaka, which we consider to be the better of the two equilibrium SPR estimates because it was corrected for size selection, is fairly close to the independently derived estimate of dynamic SPR. Although this is perhaps fortuitous, it at least suggests that both estimates are relatively unbiased.

We believe, however, that if the necessary parameters could be estimated with sufficient accuracy then the equilibrium estimate would prove to be the less biased of the two. To this end, one of our primary goals for future research is to improve the methods for ageing bottomfishes so that the traditional age-based methods for estimating growth and mortality can be used with confidence.

Are Species Overfished?

Based solely on the criterion that a species is overfished when SPR < 0.20, we conclude that none of the species is presently overfished (Table 1). However, considering that there is a large uncertainty in the estimates of SPR and four of the five species had values of dynamic SPR less than 0.30, it would be at least prudent to consider some form of management likely to increase the spawning biomass, perhaps to a value near 0.30, which is considered by Beddington and Cooke (1983) and Goodyear (1989) to be optimum.

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Table 1.--Estimates of the equilibrium and dynamic spawning potential ratios (SPRs) for bottomfishes in the main Hawaiian Islands (MHI) and the Northwestern Hawaiian Islands (NWHI). For each equilibrium estimate are shown the values of Z/K, M/K, and L_∞ used in the calculation. For the equilibrium estimate of opakapaka SPR, the logistic selection model was used to determine l_e in text Equation (1) and L_c for the Wetherall procedure (Wetherall et al. 1987) of estimating Z/K, M/K, and L_∞. For the dynamic estimate of opakapaka, the logistic selection model was used to estimate the s_i in text Equation (5). In both cases, the consequences of using the logistic selection model on the value of SPR are indicated in the table.

Species	MHI		NWHI		SPR
	Z/K	L_∞	M/K	L_∞	
Equilibrium SPR					
Opakapaka	2.5	75.1	6.3	87.4	--
** logistic selection	--	--	1.4	75.1	31.0
Onaga	1.9	89.5	3.0	92.9	--
Ehu	5.4	76.9	2.8	68.9	21.2
Uku	--	--	--	--	--
Ulua	--	--	--	--	--
Dynamic SPR					
Opakapaka	--	--	--	--	25.0
** logistic selection	--	--	--	--	29.3
Onaga	--	--	--	--	25.8
Ehu	--	--	--	--	29.5
Uku	--	--	--	--	40.0
Ulua	--	--	--	--	25.4

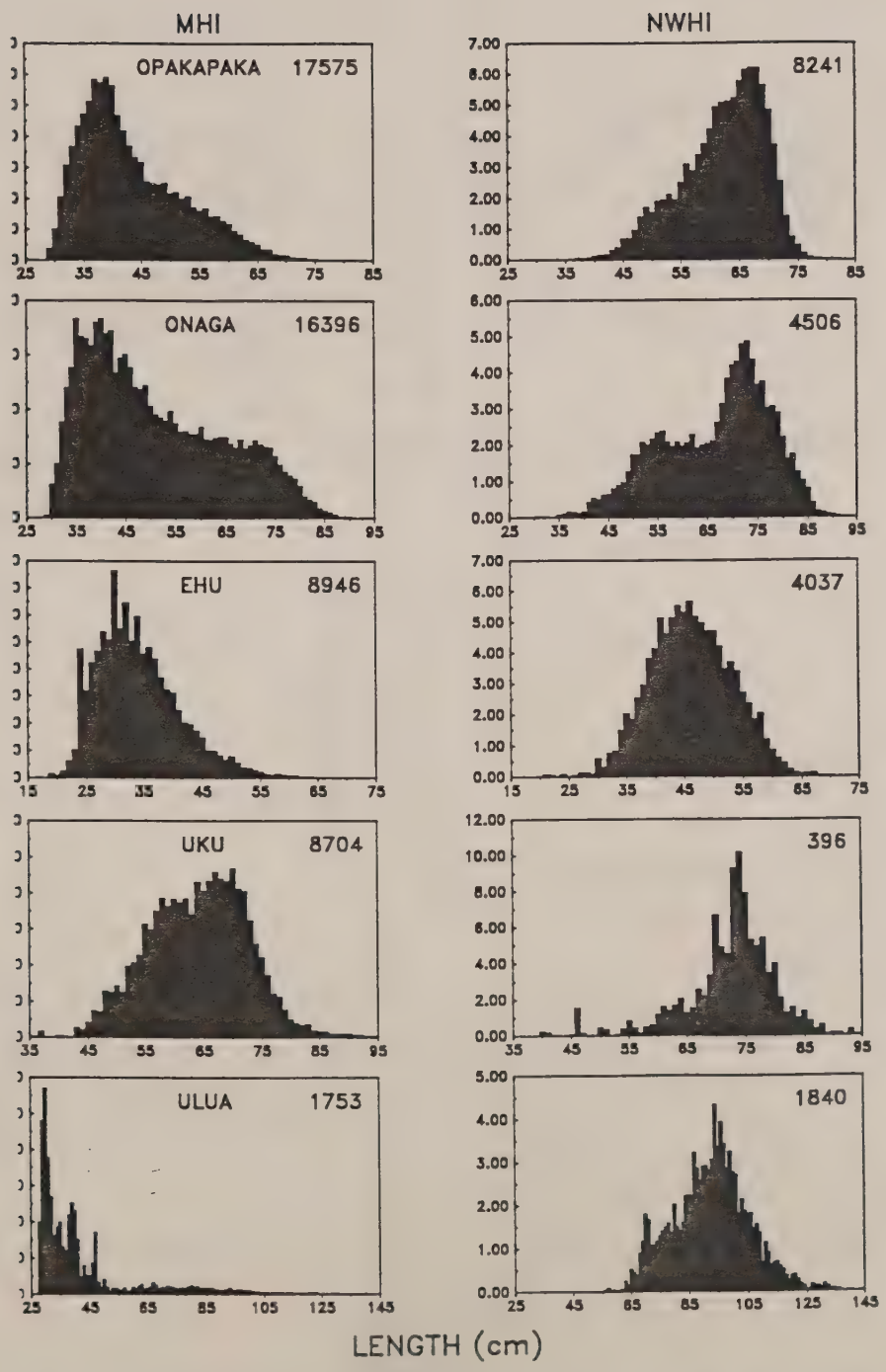

Figure 1.--Length-frequency distributions for each of the five species of bottomfishes in the main Hawaiian Islands (MHI) and in the Northwestern Hawaiian Islands (NWHI). Each distribution is based on the number of lots shown in the upper right corner of the plot.

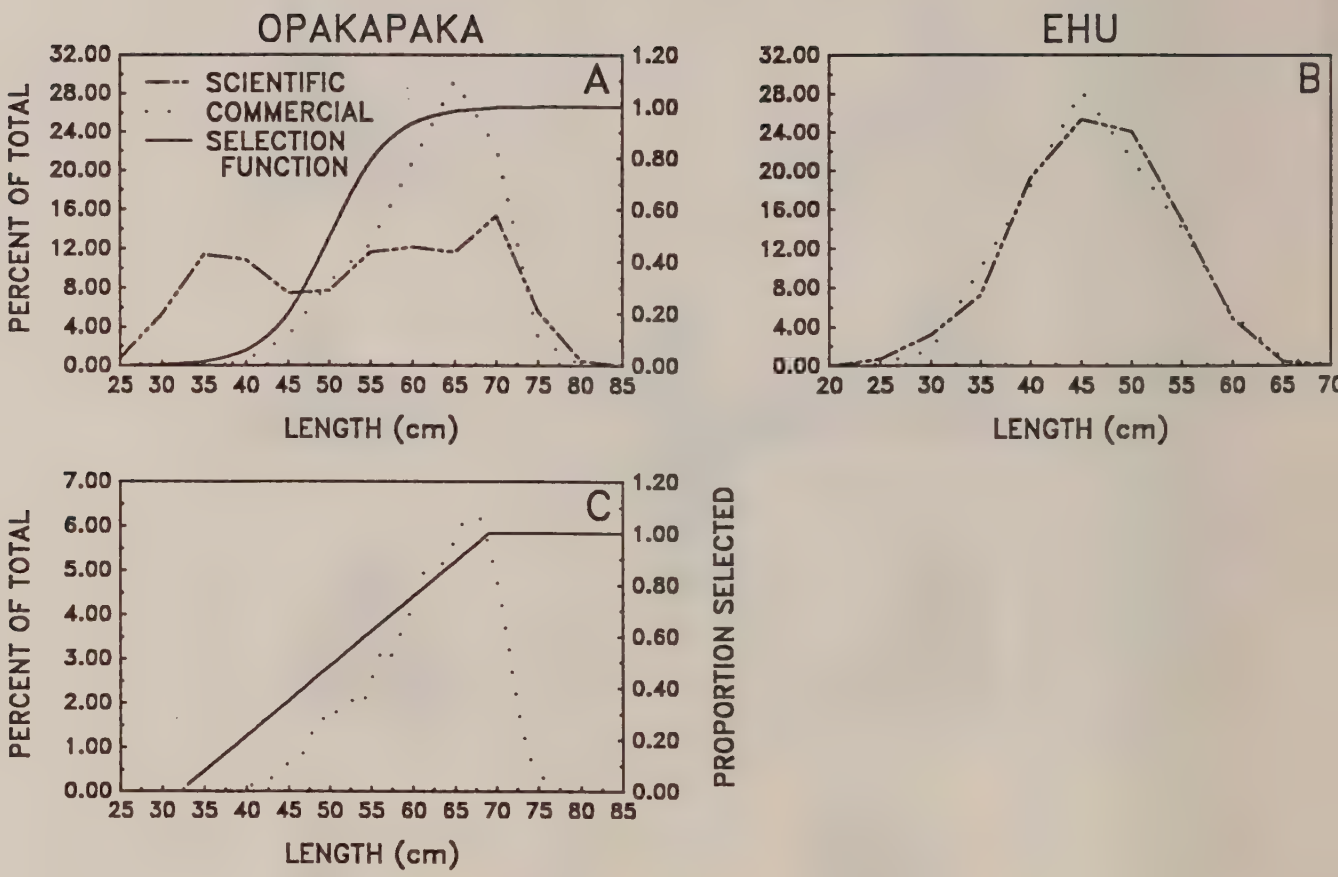

Figure 2.--Length-frequency distributions of the commercial catch and of the random scientific samples obtained on the NOAA ship *Townsend Cromwell*: (A) opakapaka and (B) ehu. For opakapaka, selection functions based on (A) the logistic model and (C) the straight line model are shown with the appropriate length-frequency data.

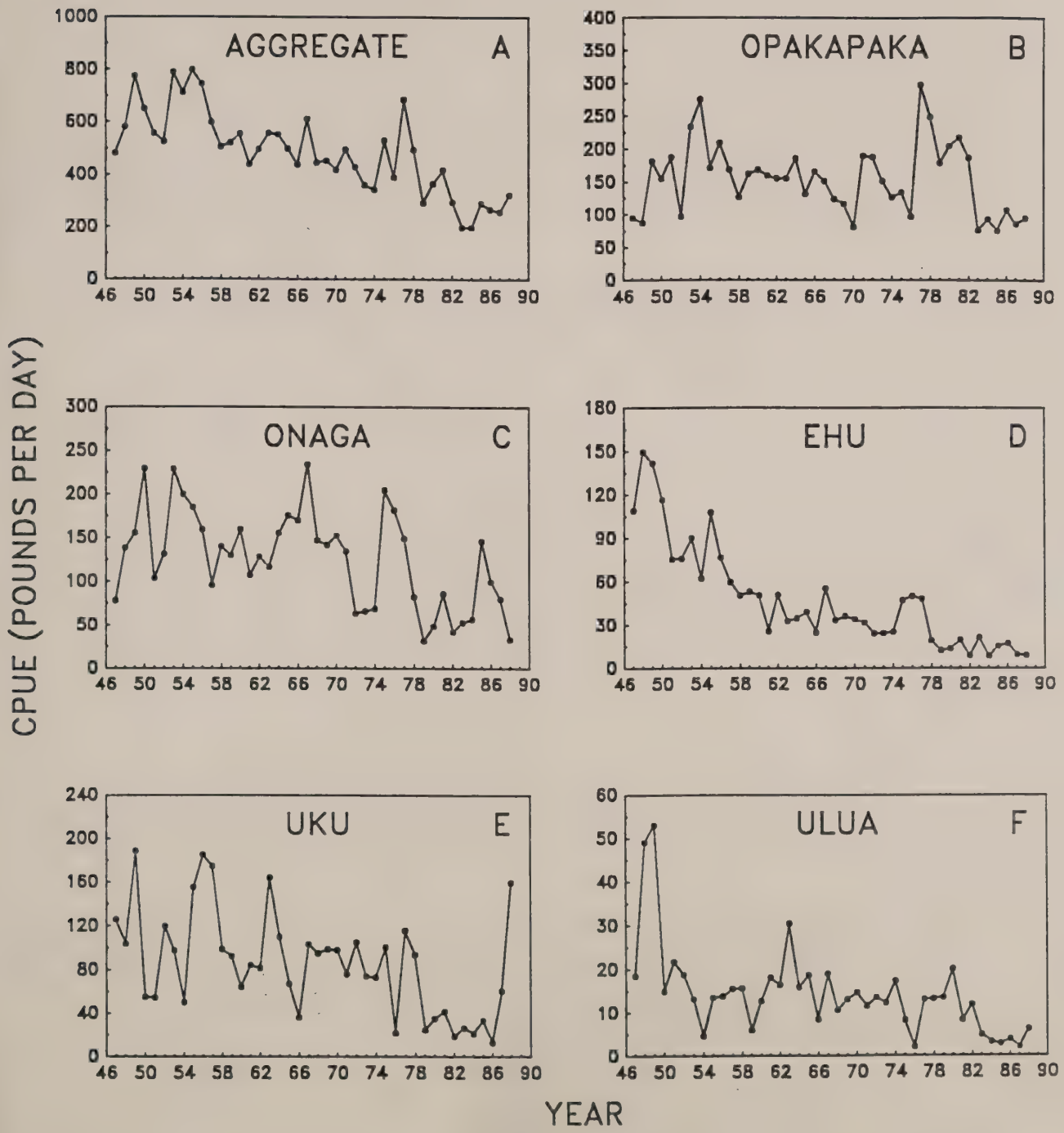

Figure 3.--Catch (in pounds per fishing day) by year for the aggregate catch of all bottomfishes (excluding kahala) and by individual species.

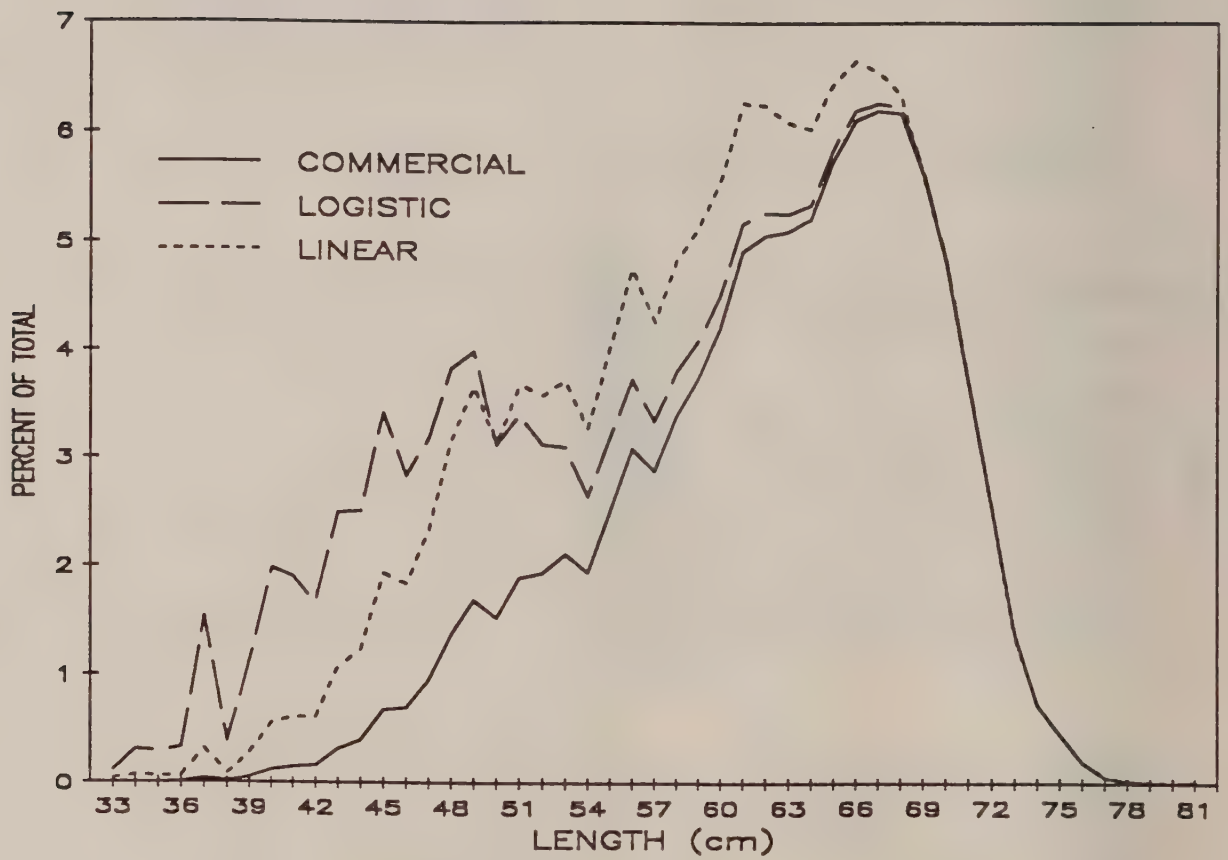

Figure 4.--Length-frequency distribution for opakapaka from the Northwestern Hawaiian Islands: uncorrected for size selection by the commercial fishery, corrected using the logistic model of size selection, and corrected using the linear model of size selection.

Appendix A.--Expressing the equilibrium spawning potential ratio (SPR) in terms of F/K, M/K, l_c, and l_m.

Although an equivalent form of text Equation (1) has been developed by Jeffrey J. Polovina (Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, 2570 Dole St., Honolulu, HI 96822-2396, unpubl. data), neither the equation nor its derivation has been published in a readily accessible form. Because of the utility of text Equation (1) in situations where the parameters are estimated using a length-based method, its derivation is included here.

The derivation starts with a slightly modified version of the age-based equation for $SSBR_f$ presented in Polovina (1987, p. 511).

$$SSBR_f = R\, e^{-Mt_c}\, e^{-(F+M)(t_m - t_c)} \int_{t_m}^{\infty} w(t)\, e^{-M(t-t_m)}\, dt \;, \qquad (1)$$

where $w(t)$ is the von Bertalanffy growth equation in terms of weight and all other symbols are the same as defined in the text. The equation for $SSBR_u$ is derived from Equation (1) by setting $F = 0$. Both equations are integrated after substituting the Beverton and Holt (1957) cubic approximation to the weight function; that is,

$$w(t) = W_\infty \sum_{n=0}^{3} \Omega_n\, e^{-nK(t-t_0)} \;; \qquad (2)$$

where $\Omega_n = 1, -3, 3, 1$ for $n = 0, 1, 2, 3$. The SPR is then expressed, in terms of age, as the ratio of these solutions:

$$SPR = e^{-F(t_m - t_c)} \, \frac{\sum_{n=0}^{3} \dfrac{\Omega_n\, e^{-nK(t_m - t_0)}}{F + M + nK}}{\sum_{n=0}^{3} \dfrac{\Omega_n\, e^{-nK(t_m - t_0)}}{M + nK}} \qquad (3)$$

Appendix A.--Continued.

The time dependency is re-expressed in terms of length dependency as follows:

Since

$$l_t = L_\infty(1 - e^{-K(t-t_0)}) \tag{4}$$

then

$$e^{-nK(t_m - t_0)} = (1 - \frac{l_m}{L_\infty})^n \tag{5}$$

and

$$e^{-F(t_m - t_c)} = (\frac{L_\infty - l_c}{L_\infty - l_m})^{-F/K} \tag{6}$$

Substituting Equations (5) and (6) into Equation (3) and dividing both numerator and denominator by $1/K$ results in the desired expression for text Equation (1).